ADAPTIVE ASPECTS OF ACTIVITY RHYTHMS IN BATS[1]

GEORGE DeCOURSEY AND PATRICIA J. DeCOURSEY

Zoophysiological Institute, University of Tübingen, Germany, and the Zoology Department, University of Wisconsin, Madison 6, Wisconsin

A daily cycle of activity in animals was first noted centuries ago, but only in the past decade has substantial progress been made in analyzing the complex interaction of physiological and environmental regulatory factors. Research in circadian physiology indicates that an endogenous timing system, coupled with some daily recurring agent of the environment, provides the basis for activity rhythm regulation of many species (Aschoff, 1958, 1960; DeCoursey, 1961; Pittendrigh, 1960). For some of the remaining problems, bats afforded several unique and promising approaches. Since bats are strongly nocturnal, but generally depend upon auditory rather than visual stimuli (Griffin, 1958), they were of particular interest for determining the effectiveness of the daily light cycle as an activity synchronizer. Furthermore, their preference for roosting in caves, and dimly lit buildings, provided opportunities for studying environment-testing behavior, and for demonstrating the ecological value of circadian rhythms. Results are presented here for experiments in the laboratory and in natural habitat.

The research was carried out under the auspices of the Zoophysiological Institute of the University of Tübingen, Germany; it is a pleasure to acknowledge the generous assistance of the Director, Professor F. P. Moehres. We extend our thanks also to the Institute's staff for help with many phases of the work; to Dr. Rolf Gögel, Pastor in Wendelsheim, Germany, for his hospitality and cooperation which made possible the studies of the *Myotis myotis* colony; to Professor Jürgen Aschoff of the Max-Planck Institute, Erling, Germany, for making available recording apparatus; to Professor Leo Pardi of the University of Turin, Italy, for help in collecting the *Rhinolophus;* and to the Zoology Department of the University of Wisconsin, especially to Professor John Emlen, for furnishing working accommodations during the preparation of the manuscript. Dr. James King and Dr. Horst Schwassmann gave helpful suggestions for the manuscript. Financial support was granted to the senior author through Public Health Fellowship No. BF-11,999 from the National Institute of Neurological Diseases and Blindness, of the United States National Institutes of Health.

Part I: Experimental laboratory studies

Material and methods

The greater European horseshoe bat, *Rhinolophus ferrum-equinum*, can be maintained in small rooms over long periods of time in good health, and its daily

[1] Present address: Zoology Department, Washington State University, Pullman, Washington.

activity accurately recorded without restriction of the animals to cages. Experiments were based upon three individuals collected from a cave in hibernating condition. In the laboratory the bats were first trained to fly to a screen-wire platform to obtain mealworms and water from small dishes.

Two smooth-walled, light-proof rooms were used in measuring activity rhythms of individual bats. Temperatures were held as uniform as possible (Figs. 1 and 2). Light schedules were provided by a 40-watt incandescent bulb and an electric timer. The rooms were entered at irregular intervals of 1–10 days for changing food and water (indicated on Figures 1 and 2).

The recording method in these two rooms took advantage of the free-hanging roosting habit of *Rhinolophus*. A string perch, used consistently by a bat, was

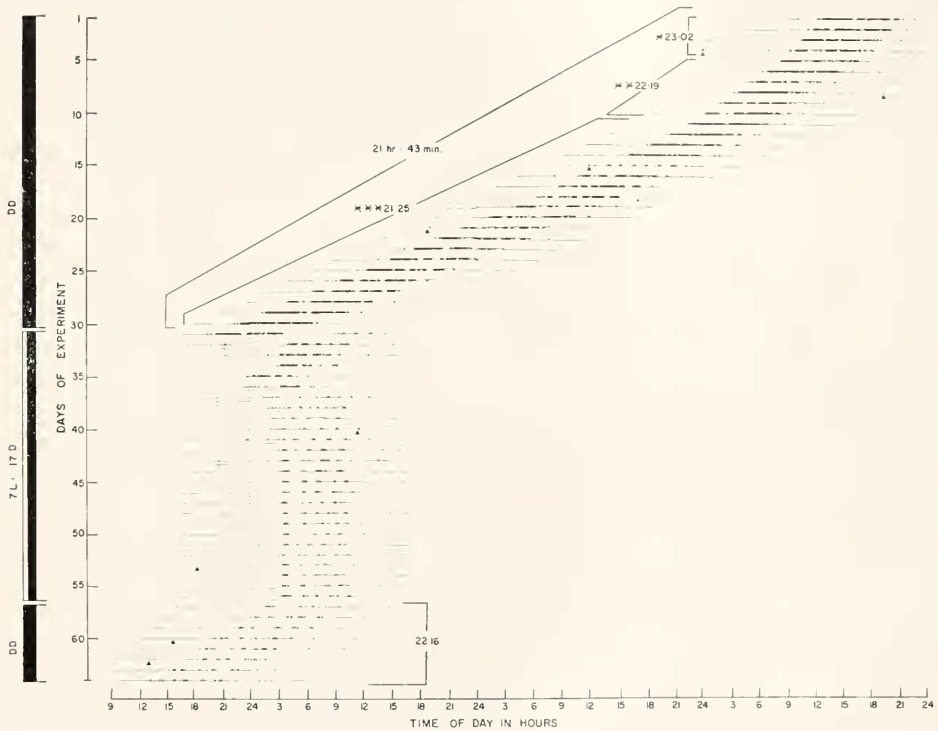

FIGURE 1. Light synchronization experiment with *Rhinolophus* #2: DD on days 1–30 → 7L:17D on days 31–34 → DD on day 35 → 7L:17D on days 36–56 → DD on days 57–64. Note day 35 in DD to distinguish masking effect of the light schedule. Nomenclature in the figures and text follows Pittendrigh (1960): DD, continuous darkness; *x*L:*y*D, a light schedule with *x* hours of light and *y* hours of darkness. Each single mark of the recorder pen represents a flight from the roosting string and return; blocks indicate frequent, short flights. Light during the artificial day schedule is shown by underlining, feeding in the light by △, and feeding in the dark by ▲. Temperature range: 22°–27° C., usually less than 2° C. fluctuation per day. Cycle length of the rhythm in DD is indicated by bracketed numbers, with the changing cycle length on days 1–30 emphasized by the three subdivisions *, **, ***. Extended time scale and splicing of the record are used for convenience in studying the frequency. For further explanation see text.

attached to a microswitch for registering flight and rest activity on an Esterline-Angus Operations Recorder. Daily segments were subsequently mounted in chronological order for graphic portrayal (Figs. 1 and 2).

A third light-proof room housed a large, darkened, artificial bat cave. The cave was a U-shaped plywood tunnel with arms 3.7, 2.1, and 1.3 meters in length, respectively, and 0.6 by 0.6 meters in cross-section. At the closed end a partial partition created a small chamber where the bats could hang from a screen-wire grid. All other footholds in the tunnel were excluded and the entire interior was

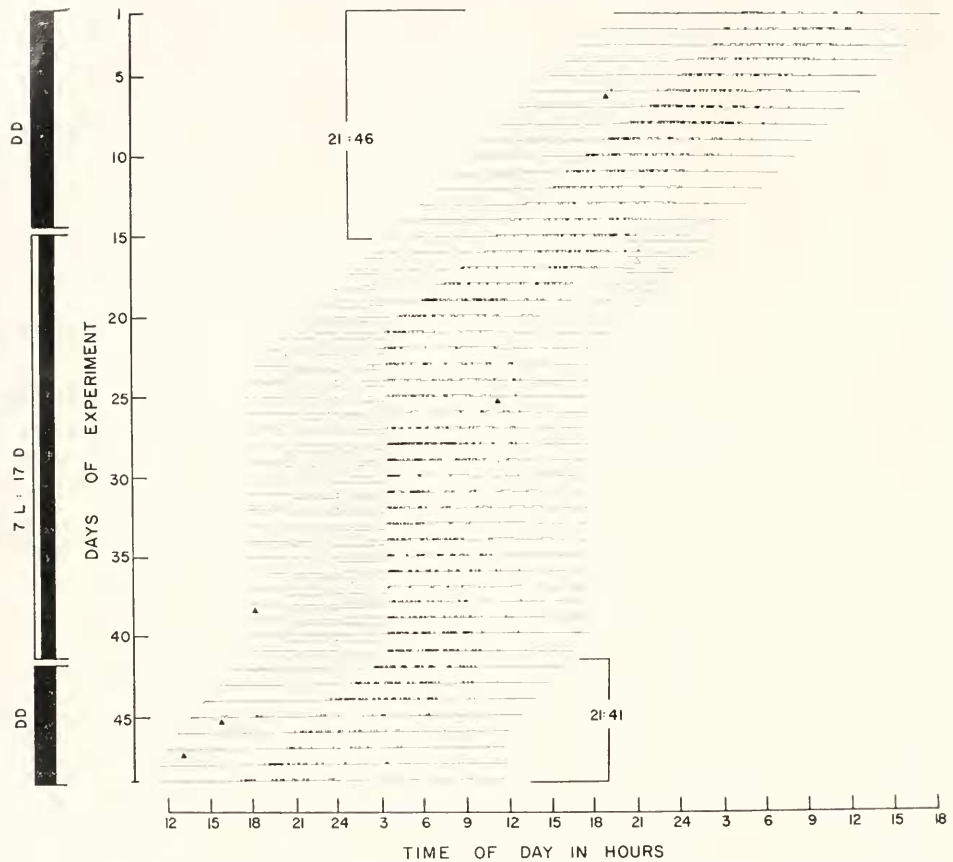

FIGURE 2. Light synchronization experiment with *Rhinolophus* #1: DD on days 1–14 ⟶ 7L:17D on days 15–41 ⟶ DD on days 42–48. Temperature range *normally* 21°–27° C. with about 3° C. variation per day; elevated baseline reflects failure of room temperature regulation, during which time the bat hung for short periods of time from a cool air vent. Other symbols as in Figure 1.

light-proofed except for the open end, then painted flat black for maximum darkening. Temperature varied between 21° and 26° C., usually less than 2° C. per day. A 40-watt overhead incandescent light and control clock supplied the room light schedule. Food and water were available *ad libitum* outside the tunnel,

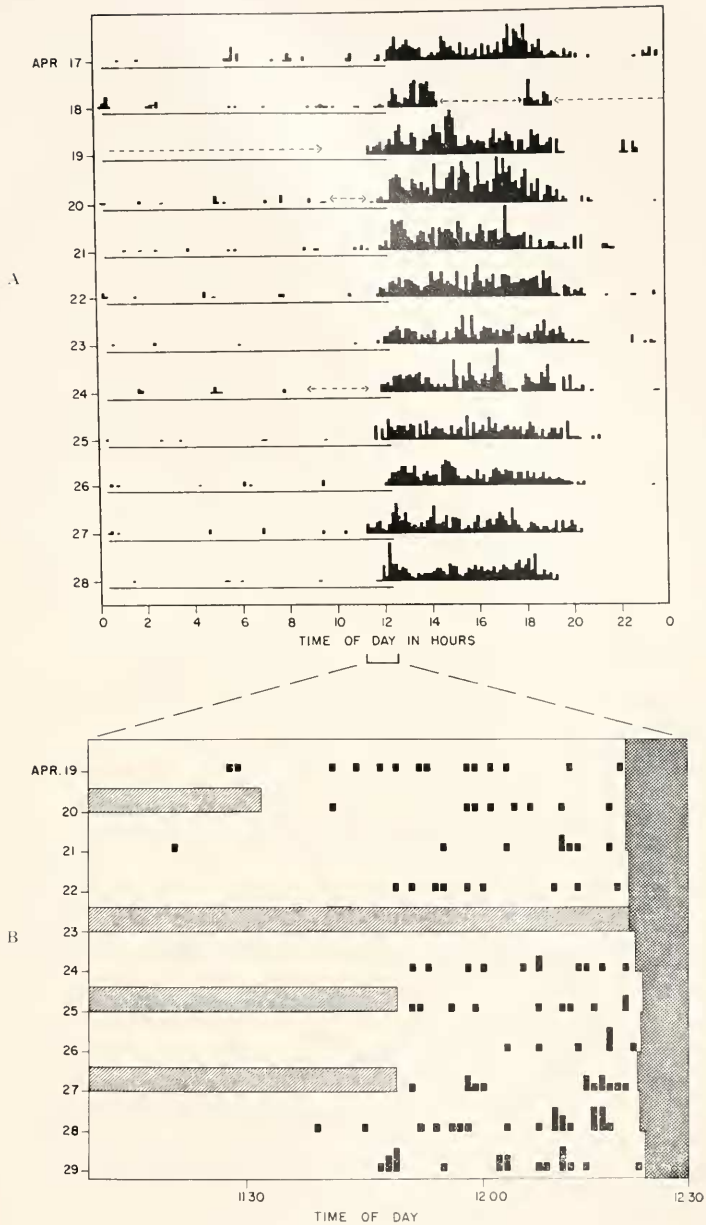

FIGURE 3. Artificial bat cave experiment, showing flight activity of *Rhinolophus* #1, 2, and 3 with constant temperature and lighting in cave, and 12L:12D in room. A. Activity from April 17–28, 1961, plotted as photocell counts/8 minutes; underlining for light hours in the room, and broken line for equipment failure. B. Activity during the time of day bracketed in A, from April 19–29, 1961, graphed as number of flights per minute up to or beyond the end of the tunnel; lack of observation shown by single hatching (no observers), or double hatching (darkness). For further explanation see text.

and were renewed by entering the room during the light period about every 5 days.

Under these conditions, the flights of the bats along the tunnel could be recorded by a dim white light beam and photocell unit near the roosting chamber. The beam was visible to a bat, while roosting, as a continuous glow, but gave no information about the day-night schedule outside the tunnel. Number of flights was tabulated on an electric counter outside the room, then photographed with an automatic camera device. An infra-red photocell unit recorded the number of flights past the open end of the tunnel; the counter was read directly for certain experiments (Fig. 3B).

Observations

A strong tool for defining which cyclic, exogenous factors are able to control the phase of an endogenous rhythm has been to change an animal from a constant environment to one in which a single factor fluctuates with 24-hour periodicity. In the first experimental series of this study, a single horseshoe bat was confined to each of the two small recording rooms, and activity first measured in DD, then in L:D, and finally again in DD (for terminology see Figure 1). The responses of the two bats (Figs. 1 and 2) were similar to those reported for a number of other nocturnal species (Aschoff, 1960; Bruce, 1960; DeCoursey, 1961, 1963; Justice, 1960; Pittendrigh, 1960; Rawson, 1959; Roberts, 1962; Stewart, 1962). The results are characterized by (1) a persistent, non-24-hour rhythm of activity in the absence of a light cycle, (2) the gradual adjustment of the time of activity during the light schedule, and (3) the ultimate establishment of a nocturnal activity pattern.

Several points merit special emphasis. The envelope of the active period, as well as the clear starting point, demonstrates the circadian nature of the rhythms in darkness. In one case the active period scanned the entire solar day in the course of several weeks (Fig. 1, top). Both inter- and intra-individual variation occurred (Figs. 1 and 2). The spectrum for these few measurements of mean cycle length (plus two additional values not shown) encompasses values from 21 hours:49 minutes to 23 hours:27 minutes. These fall in the range of values shown by comparable measurements for several species of bats (Griffin and Welsh, 1937; Menaker, 1961; Pohl, 1961; Rawson, 1960), but are much shorter than for most other nocturnal species (Aschoff, 1958; DeCoursey, 1961, 1963; Johnson, 1939; Justice, 1960; Pittendrigh, 1960; Rawson, 1959; Roberts, 1960; Stewart, 1962). Furthermore, the cycle length in any one test period may gradually change. The lability of the rhythm is particularly marked for *Rhinolophus* #2 (Fig. 1, top); also see Rawson (1960). Such a phenomenon has been observed by Menaker (1961) for bats, as part of the brief transition from the winter to the summer condition, but in this study the bats remained under the experimental conditions for many months. A variable frequency for free-running rhythms probably represents one end of a scale, ranging from the relatively stable rhythms of *Glaucomys* (DeCoursey, 1961), through the history-dependent rhythms of hamsters, finches, and cockroaches (Pittendrigh, 1960), to the extremely variable rhythms of *Muscardinus*, which may alter the period from about 25 to 20 hours (DeCoursey, unpublished experiments). The values for free-running rhythms of bats give an estimate of the magnitude of correction needed to synchronize the activity to the appropriate part of the day. The cycles of light and dark (Figs. 1 and 2, center) sufficed to bring about the necessary

correction. In both instances nocturnality was established, but, as in other species, the pattern of adjustment depended upon the relationship of light to the activity of the animal (see DeCoursey, 1961, 1963 for a discussion of this point). Nocturnal activity has also been noted for two other species of bats under laboratory conditions (Griffin and Welsh, 1937; Kowalski, 1955).

The demonstration of rhythmic activity deviating slightly from 24 hours in cycle length, for bats in a constant environment, and the subsequent locking of the phase in an L:D regime was considered conclusive evidence for regulation of activity by both endogenous and exogenous factors. Whether cyclic factors other than light are significant has not yet been extensively investigated for bats. Griffin and

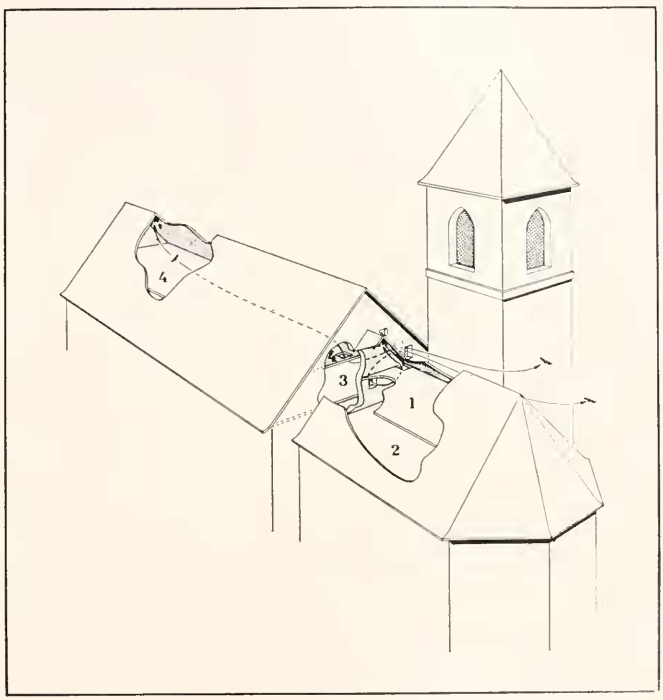

FIGURE 4. Cutaway diagram of the Wendelsheim loft. Single lines mark flight routes from roosting areas in Rooms 1 or 4 to outside of church, with broken line for that part of route not visible in diagram. See text.

Welsh (1937) suggest that feeding clues may be important for some individuals, in the absence of light clues, but Kowalski (1955) found no evidence for such a conclusion.

As a consequence of the above experiments, the question arose as to the manner in which the bats detected the environmental changes to which they would eventually synchronize their activity. In the second series of experiments, the three horseshoe bats were placed in the artificial cave room for several months with room light on at midnight and off at noon. Preliminary observations revealed that the bats hung

during the daylight hours almost exclusively in the darkened roosting chamber, then during the hours of darkness flew frequently back and forth through the tunnel. Since it was necessary for a roosting bat to fly the length of the tunnel to see the room light and gain access to the room, it was possible to determine the time of day at which such light-sampling took place.

The rate of activity, measured by the total number of flights past the counting cell per 8-minute interval, was a convenient indicator of the activity pattern. As in the first experiments, the bats remained inactive for most of the day. A few flights were made from the cave into the lighted room. All available evidence suggests that a bat, in at least the majority of cases, returned almost immediately to the roosting chamber, and therefore was exposed only momentarily to the light. The number of flights increased during the last hour of daylight, then rose sharply soon after lights out. Flight activity continued almost unabated for approximately 8 hours, tapering off well in advance of daylight (Fig. 3A).

The crucial point to note is the anticipation of the light change by these bats after the long daylight inactivity. In order to determine more exactly the number and duration of flights within the tunnel and in the room at this time, the bats and the electric counters were watched simultaneously for ½–3 hours preceding lights out, for several weeks (Fig. 3B). Usually the bats flew out into the room and circled once or twice before returning to the cave. In some cases the bats did not leave the tunnel, but turned before reaching the open end and flew back into the roosting chamber. In sharp contrast was the abrupt onset of activity for the bats in the first experimental series just after the lights out transition (compare Figures 1 and 2 with Figure 3B). The significance of these data is considered in the Discussion.

Part II: Field studies of activity in summer bat colonies

Material and methods

A summer colony of about 500 adult female *Myotis myotis* and their young was observed from June 24 to July 30, 1961, in the loft of the Wendelsheim church, Germany. Additional data were gathered from seven breeding colonies of *Myotis lucifugus* during the summer of 1962 in Madison, Wisconsin.

At the Wendelsheim loft, large sheets of transparent plastic were gradually lowered into place in order to channel the majority of the bats, in their departure and return, to a series of rooms having a pronounced light gradient (from roosting place in Room 1 to Room 2 to Room 3; see Figure 4). A secondary flight route between Rooms 4 and 3, used occasionally by a few bats, remained unchanged and was not usually observed. From the large central loft (Room 3), all bats exited through one small window, then flew down a narrow V-shaped trough formed by the tower wall and the nave roof before gaining a free flyway (Fig. 4).

From Room 3 it was possible to count departures and returns by watching the bats silhouetted through the open window against the sky. The beginning of activity in the dimmer roosting rooms was judged by direct observation, or by counting the rate of high-frequency calls of the bats at the small aperture between Rooms 2 and 3, using a microphone and oscilloscope detector (Fig. 5). At regular intervals during the evening flights, the light intensity outside the church was

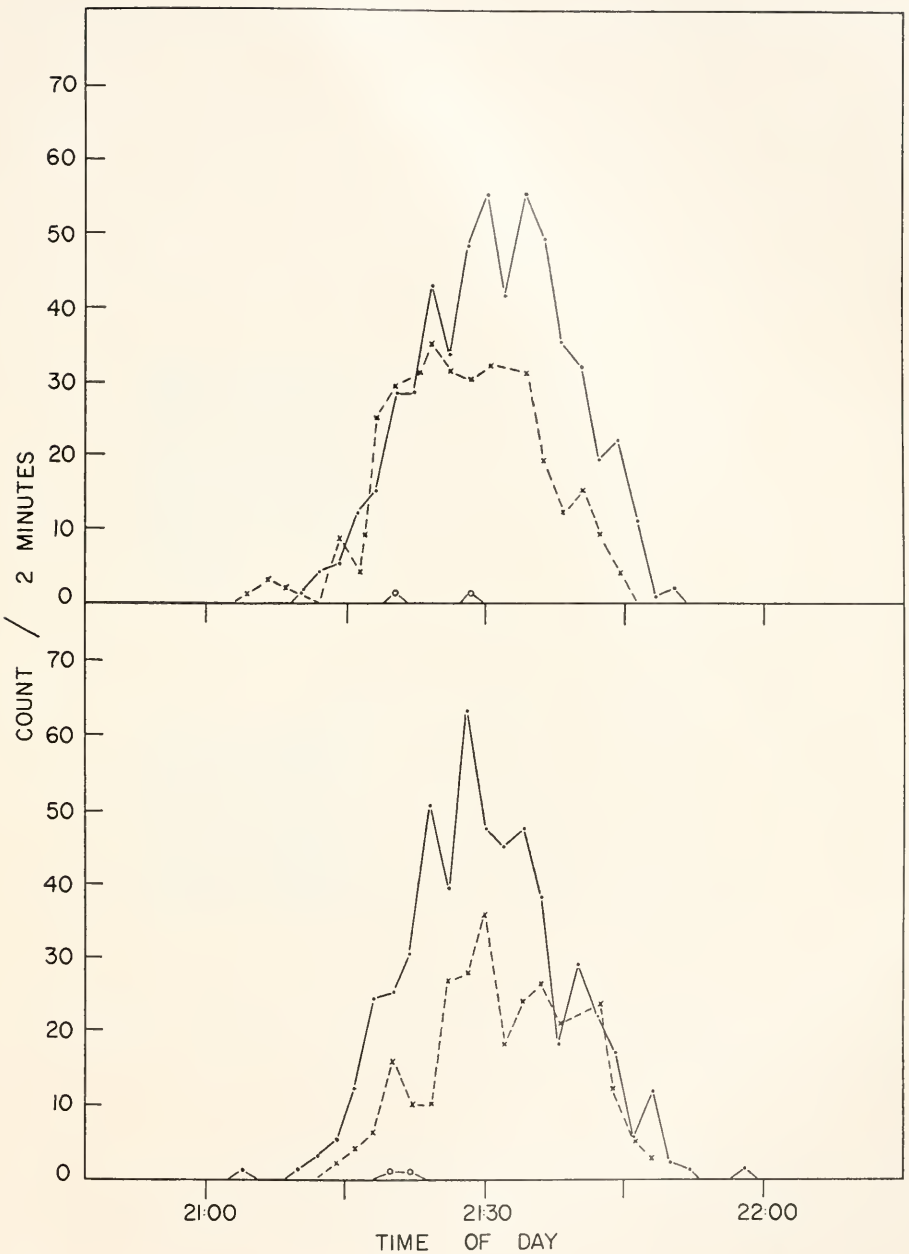

FIGURE 5. Evening activity of bats on two consecutive clear nights at Wendelsheim, July, 1961: •—• exit flights as bats/2 minutes, o—o returns to loft, x---x pre-exit flight activity estimated as the number of high-frequency calls/2 minutes at passageway from Room 2 to 3.

measured with a Lange Luxmeter. Simple recording methods were devised for counting and tabulating data *without light or noise disturbance to the bats.*

Observations

In spite of severe limitations, field studies offer possibilities for further insight into the problem of environment-sampling by the bats. Due to conspicuous colonial habits, bats are more suitable for surveillance than most nocturnal species, and have been the object of many observations. Emergence of bats from roosting places usually takes place at dusk (Allison, 1937; Church, 1957; Eisentraut, 1952; Moebus, unpublished data; Schwassmann, personal communication; Twente, 1955; Venables, 1953), often correlated with a small range of light intensities (Twente,

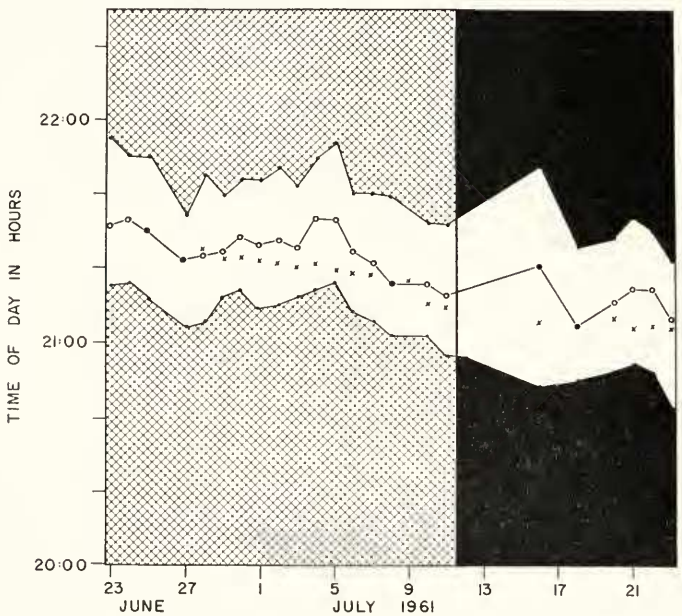

FIGURE 6. Summary for the Wendelsheim colony with white central zone indicating the flight time (exit count rising above four bats/2 minutes to count dropping below four bats/2 minutes) for the normally lighted loft at left, crosshatched, and for the darkened church at right, black. Symbols: o average exit time on clear days, and • on cloudy days, x for outdoor light intensity of 0.08 lux.

1955; Venables, 1953), but the darkness of a total eclipse during daytime did not evoke activity (Krzanowski, 1959). Exit flight times roughly parallel the time of sunset throughout the summer (Church, 1957; Moebus, unpublished data), thus implicating light as the chief synchronizer, in spite of the poorly developed vision of bats.

The Wendelsheim colony was also strictly nocturnal. After remaining relatively quietly in Room 1 or 2 during the day, the bats departed rapidly from the church about one-half hour after sunset. The flight rate rose in a few minutes to

a peak, then declined until only the young and a few adults were left in the loft (Figs. 5 and 7). Little more than an hour elapsed between the first flight activity in the roosting loft and the end of the exit flight, and the actual departure of the 500 bats usually required less than 45 minutes (Figs. 5–7). Only occasional adults were seen until shortly before dawn; then the return flight into the loft lasted

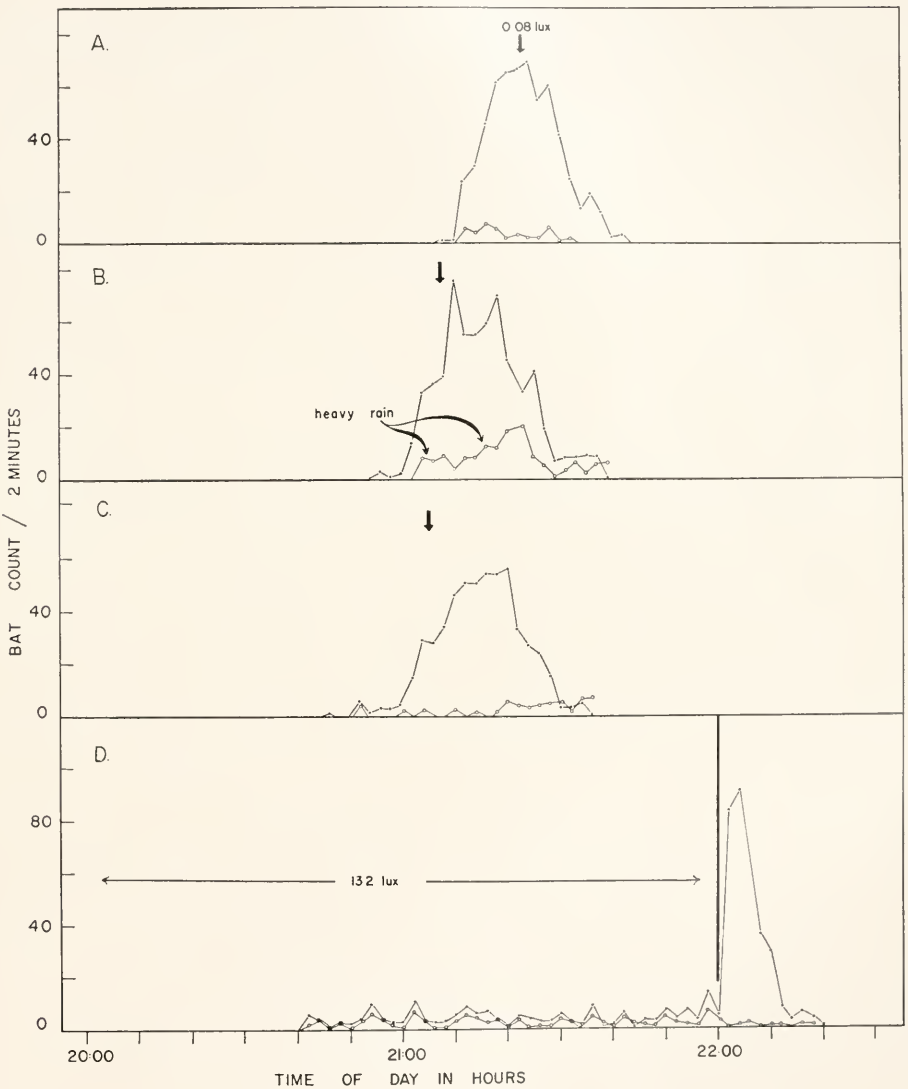

FIGURE 7. Environmental influences on activity at the Wendelsheim colony: A. Clear night in July, normal lighting. B. Rainy night in July, normal lighting. C. Clear night in August, darkened church. D. Illuminated flyway in August. Symbols: • — • exits, o — o returns, for outdoor light intensity of 0.08 lux.

slightly longer than the evening flight. Similarly, in Madison, great numbers of bats left attic roosting retreats in many old houses, and flew towards the lake in search of food. Due to the synchrony of the exiting bats, it was possible to locate several new colonies in a single evening merely by following the stream of bats at dusk back to the source. The counts at several colonies showed a pattern almost identical to the Wendelsheim flights, illustrated in Figure 5.

These observations also illustrated the close link between activity time and specific light intensities. In the normally lighted loft at Wendelsheim *average exit time* took place between 0.02 and 0.10 lux, with a mean value of 0.05 lux. No light meter was available in Madison, but on heavily overcast days the flight started five or ten minutes earlier. With the shortening days in July and August, the flights also began earlier, both at Wendelsheim (Fig. 6) and in Madison.

Other exogenous factors had only a minor influence. Daytime restlessness inside the Wendelsheim loft increased on hot, sunny days. Heavy rain often thoroughly disrupted the evening flight (Fig. 7B). After July 11, the young bats, recognizable by their uncertain flying, left with the adults but soon landed on the exterior walls; many crawled back into the church through the window. The increasing number of returns after mid-July, during or shortly after the exit flight, was attributable to the young (Figs. 7A and 7C). Thus, several meteorological and biological factors influenced the amount of activity to a small extent, but light seemed the chief synchronizer of activity throughout the season.

The sampling behavior (Twente, 1955) of the bats prior to the exit flight was apparently the means of testing the light intensity. Soon after leaving the roosting room at the Wendelsheim colony, the bats flew towards the exit window, often hovering there momentarily. The circling continued until one bat darted out the window, followed in rapid succession by many others (Fig. 5).

In order to further evaluate the importance of light sampling in a colony under natural conditions, an experiment was conducted at Wendelsheim. In the loft rooms, as many light leaks as possible were covered. This darkening and the initial structural changes (see Material and Methods) essentially duplicated the laboratory cave experiments, by requiring a bat, after arousal, to fly through the series of rooms to the exit window, to see if conditions were propitious for flight. The light intensity in the loft was reduced many-fold, but it unfortunately proved unfeasible to eliminate all the minute light leaks between the roof tiles. Neither earlier activity in the roosting room, nor earlier sampling resulted, nor was the timing of the exit flight affected (Figs. 6 and 7C). A second experiment was conducted on one evening, several weeks later. The V-shaped trough just outside the exit window was illuminated with a powerful floodlight (Fig. 4), from one-half hour before the usual start of the exit flight to one hour after expected peak exit time. As the normal departure time arrived the sampling became very intense and continuous, with large numbers of bats hovering near the window. A few flew out into the bright area but 67% re-entered the loft, most of them immediately. More adequate lighting of the outside of the church would probably have totally prevented exits. After lights out, the bats in the loft whirled and circled for a few seconds and then poured out through the window (Fig. 7D). In one of the few parallel field experiments, Hodgson (1955) was able to delay the departure of ants from an underground nest by covering the approaches at dawn with dark awnings, or

conversely, by hanging a lantern above the nest before dawn, caused an early departure.

Discussion

The hypothesis that the daily activity of an animal depends upon an endogenous timer and clues of the environment is not peculiar to bats. In one sense, this example merely broadens the comparative base of a well grounded theory (significant examples or reviews in Aschoff, 1963; Bruce, 1960; Bünning, 1963; DeCoursey, 1960; Pittendrigh, 1960; Rawson, 1959). Bats were useful, however, for considering how an animal compensates for an endogenous timer which chronically runs too fast or too slow, and what useful purpose such built-in variability serves.

The exogenous clues are the sensory stimuli which set in action processes for holding the activity rhythm in appropriate phase with the environment. A synchronizer in its simplest form consists of two intensity extremes with transition zones between the two: for most animals a daytime condition of high light intensity followed by an abrupt twilight change to a dim night state, and a return to the daytime state. Sensory input may be dependent upon one or both transitions or upon the steady-state light intensity. These alternatives are over-simplifications for the sake of clarity, since effective synchronizers are known, ranging from those with instantaneous changes between the two steady-states, to near sinusoidal changes from maximum to minimum intensity (Swade, unpublished data). Furthermore, both continuous action and transitional type signals may contribute.

The present work gives little information on the time of actual correction of an endogenous element (see Aschoff, 1963 for further discussion of this problem). The laboratory and field experiments imply, however, that bats receive their sensory input primarily from the dusk transition of the environment. The animals living in the cave anticipated the light change and flew out briefly to sample. In contrast, the same individuals, hanging in a room with a full view of the light, started activity almost simultaneously with the beginning of darkness. By the same reasoning, a much earlier start of sampling at the Wendelsheim colony after the darkening of the loft should be expected. This was not the case, possibly due to inadequate darkening.

The ecological usefulness of this non-24-hour, endogenous rhythmicity has been touched upon in the course of the preceding discussion. The disadvantages of a purely exogenous regulation of activity are particularly pronounced in the case of bats, but are probably pertinent to all cave- and hole-dwelling species as well. Bats are often torpid during much of the daytime inactive period, appearing uncoordinated and unresponsive to auditory, tactile or visual stimuli. Even if awake and alert they are not exposed to the environment when they roost in unlighted retreats. At the other extreme, the question arises why animals did not develop a purely endogenous system. The majority depend upon both exogenous and endogenous regulators. The endogenous entity may act as a wake-up timer to insure arousal of the bat and the regaining of its full sensory capacities before it tries to perceive its environment. It is perhaps easier in terms of selection to evolve a simple, rather crude timer, capable of correction by the external environment, than to produce one complex enough to predict and account for daily and seasonal changes of the solar day-night cycle.

Conclusions and Summary

Bats living under laboratory or field conditions manifested precise nocturnal activity rhythms. Light-sampling at the light-to-dark transition was apparently the chief means of synchronizing an endogenous, non-24-hour activity rhythm to the daily light cycle.

1. Two horseshoe bats, free-living in separate, small recording rooms, readily adjusted the time of activity to correspond to an L:D schedule.

2. Three horseshoe bats, roosting in a darkened tunnel with no direct view of the 12L:12D schedule of the outside room, anticipated the light-dark change by flying out regularly during the hour before the lights were turned out, then were active for about 8 hours.

3. A colony of *Myotis myotis* exited from a church loft at an average light intensity of 0.05 lux and returned at dawn. Attempted darkening of the church did not result in earlier light-sampling. Illumination of the flight path at the normal exit time resulted in intense sampling but prevented the actual departure of most of the bats.

LITERATURE CITED

Allison, V. C., 1937. Evening bat flight from Carlsbad Caverns. *J. Mammal.*, **18**: 80–82.

Aschoff, J., 1958. Tierische Periodik unter dem Einfluss von Zeitgebern. *Zeitschr. f. Tierpsychol.*, **15**: 1–28.

Aschoff, J., 1960. Exogenous and endogenous components in circadian rhythms. *Cold Spring Harbor Symp. Quant. Biol.*, **25**: 11–28.

Aschoff, J., 1963. Comparative physiology: diurnal rhythms. *Ann. Rev. Physiol.*, **25**: 581–600.

Bruce, V. G., 1960. Environmental entrainment of circadian rhythms. *Cold Spring Harbor Symp. Quant. Biol.*, **25**: 29–48.

Bünning, E., 1963. Die physiologische Uhr. Springer Verlag, Berlin; 153 pp.

Church, H. F., 1957. The times of emergence of the pipestrelle. *Proc. Zool. Soc. London*, **128**: 600–602.

DeCoursey, P. J., 1960. Phase control of activity in a rodent. *Cold Spring Harbor Symp. Quant. Biol.*, **25**: 49–55.

DeCoursey, P. J., 1961. Effect of light on the circadian activity rhythm of the flying squirrel, *Glaucomys volans*. *Zeitschr. f. vergl. Physiol.*, **44**: 331–354.

DeCoursey, P. J., 1963. Function of the light response curve in hamsters. *J. Cell. Comp. Physiol.*, (in press).

Eisentraut, M., 1952. Beobachtung über Jagdroute und Flugbeginn bei Fledermäusen. *Bonner. Zool. Beit.*, **3**: 211–220.

Griffin, D. R., 1958. Listening in the Dark. Yale University Press, New Haven; 413 pp.

Griffin, D. R., and J. H. Welsh, 1937. Activity rhythms in bats under constant external conditions. *J. Mammal.*, **18**: 337–342.

Hodgson, E. S., 1955. An ecological study of the behavior of the leaf cutting ant *Atta cephalotes*. *Ecology*, **36**: 293–304.

Johnson, M. S., 1939. Effect of continuous light on periodic spontaneous activity of white-footed mice (*Peromyscus*). *J. Exp. Zool.*, **82**: 315–328.

Justice, K. E., 1960. Nocturnalism in three species of desert rodents. Ph.D. Thesis, University of Arizona.

Kowalski, K., 1955. The daily rhythm of activity in the mouse-eared bat (*Myotis myotis* Borkh.). *Folia biol. Warszawa*, **3**: 55–64.

Krzanowski, A., 1959. Behavior of bats during the total solar eclipse in Poland on June 30th, 1954. *Polska Akademia Nauk, Acta Theriologica*, **2**: 281–283.

Menaker, M., 1961. The free running period of the bat clock; seasonal variations at low body temperature. *J. Cell. Comp. Physiol.*, **57**: 81–86.

Pittendrigh, C. S., 1960. Circadian rhythms and the circadian organization of living systems. *Cold Spring Harbor Symp. Quant. Biol.*, **25**: 159–184.

Pohl, H., 1961. Temperaturregulation und Tagesperiodik des Stoffwechsels bei Winterschläfern. (Untersuchungen an *Myotis myotis* Borkh., *Glis glis* L. und *Mesocricetus auratus* Waterh.) *Zeitschr. f. vergl. Physiol.*, **45**: 109–153.

Rawson, K. S., 1959. Experimental modification of mammalian endogenous activity rhythms. *In:* Photoperiodism and Related Phenomena in Plants and Animals, Edit. by H. Withrow. A. A. A. S., Washington, D. C.

Rawson, K. S., 1960. Effects of tissue temperature upon diurnal rhythms. *Cold Spring Harbor Symp. Quant. Biol.*, **25**: 105–113.

Roberts, S. K., 1960. Circadian activity rhythms in cockroaches. I. The free-running rhythm in steady state. *J. Cell. Comp. Physiol.*, **55**: 99–110.

Roberts, S. K., 1962. Circadian rhythms in cockroaches. II. Entrainment and phase shifting. *J. Cell. Comp. Physiol.*, **59**: 175–186.

Stewart, M. C., 1962. Preliminary investigation of circadian rhythms in the pocket mouse *Perognathus intermedius*. M.S. Thesis, University of Wisconsin.

Twente, J. W., Jr., 1955. Some aspects of habitat selection and other behavior of cavern dwelling bats. *Ecology*, **36**: 706–732.

Venables, L. S., 1953. Observations at a pipistrelle bat roost. *J. An. Ecol.*, **12**: 19–26.